A PRELIMINARY CORAL REEF ECOSYSTEM MODEL

Edited by

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A major goal of the CITRE planning effort was to develop a conceptual framework for a systems model of a coral reef ecosystem suitable for computerization. Both the process of development and the preliminary results may be of some value to future comprehensive studies of complex reef systems.

The preliminary model was conceived not only to outline a possible mathematical model, but also to integrate the proposed research of many specialists into a coherent framework with defined interactions. While the specialists generated the model structure, they also had to modify their research plans to incorporate all major aspects of the system as identified in the model.

No one model can deal with all aspects of an ecosystem. Its properties, however, should ultimately resemble those of the system being modeled and its level of abstraction should suit its intended purpose. Thus no model is static; it must evolve as available knowledge of the ecosystem increases. The preliminary model described here is one fixed point in such an evolving process. It represents an intermediate level of ecological abstraction, which, because of the diversity of the reef system, is nevertheless highly complex. It is based on the great diversity of viewpoints and professional experiences of the investigators involved. Yet, while its details are open to question, it represents a useful benchmark from which to proceed.

The model was developed during a two-week workshop at Glover's Reef, British Honduras, in November 1971. Forty-one participants (see Introduction) representing a wide variety of reef-related disciplines and with experience in many coral reef areas attended this workshop. The principal activity was the development of a conceptual model sufficiently comprehensive that it could be applied to most reef areas. However, the shallow reef flat areas of Glover's Reef served as the prime focus for the initial effort and this may be reflected in some of the details presented here. Overall, the result represents a unique synthesis of current information about the tropical reef ecosystem.

Process of Model Development

CITRE participants were initially chosen to be members of one or more of the nine working groups (Introduction) with responsibility for a major aspect of coral reef ecology. Most working groups met before the workshop for initial discussion of their subject area and an introduction to modeling concepts. The workshop itself included lectures introducing the scientists to some aspects of modeling theory, and presentations by working groups as they fitted their subject matter into the general modeling framework. The working groups proceeded by internal discussions, consultations with the modelers and with other working groups, and field observations to check on the general applicability of the model elements developed. The minor inconveniences of working at a remote site were far outweighed by the freedom from distractions and the ability to "consult the environment."

The model was designed to depict the flow of carbon through the coral reef ecosystem. Each working group first defined the "compartments," or functional units between which the flows were to be measured. An approximate limit of twenty compartments per working group was set to fix the overall model complexity within present computer capabilities. Inter-group discussions resolved problems of overlapping or overlooked functional units. Diagrams were then developed for each compartment relating it to other compartments and flows in the system. The compartments were listed in a matrix, and the interactions between compartments determined jointly by the working groups involved. Some quantification of these interactions was attempted (at least in terms of orders of magnitude), but this was not completed and is omitted here. Revisions and adjustments continued throughout the workshop. The terrestrial section was kept simplified as the primary concern was its interactions with the reef system.

The model developed through a cyclical progression. A statement of the purpose of the model and the definition of compartments was followed by the conceptualization of the initial model and field observations to check the model validity, leading to changes in the conceptualization and (more rarely) in compartment definitions. With each permutation the model became more refined and (hopefully) accurate.

The Model

Compartments

Three basic elements characterize the model: compartments, flows (fluxes) and external driving forces (forcing functions). The compartments are the carbon or carbon-equivalent storage units of the system and may be defined as plant or animal types that act as processing units for the food which they ingest or produce, or as material pools such as detritus or carbon dioxide through which substances pass as they cycle in the system. Compartments in the CITRE model may be considered "functional groups" in that they are abstract condensations of groups of organisms or substances that apparently have the same or similar functions in the ecosystem. In this sense they are "ecological species" as opposed to conventional taxonomic species. For example, Halimeda, Penicillus, Rhipocephalus, Udotea, Jania, and Corallina are distinct genera of algae (even belonging to two phyla); yet in the model they are all considered part of the same compartment--the noncrustose, calcium carbonate-producing macroalgae designated XCBALG* [6] (see Table I). Likewise two compartments are distinguished on whether motile organisms remove solid substratum as they feed ("scrapers": designated XSCRAP [35]), or eat only the overlying organisms ("browsers": XBROWS [36]). All dissolved organic compounds containing nitrogen, and not associated with some other compartment, are similarly grouped (XDON [67]).

Compartment boundaries not only combine dissimilar species on functional grounds, in some cases they even separate parts of organisms with distinct roles or locations. Marine grass blades (XBLADE [9]) were separated from marine grass roots (XROOT [10]) because of the functional differences inherent in the location of these parts above versus below the sediment surface. Transport from one part of the plant to another thus becomes a flow between compartments. When it appeared that the inorganic carbon cycle could be most easily treated as a distinct system, separate compartments were established for the calcium carbonate in the walls of living organisms (XORG [84]) and the remaining (organic) carbon in the organisms. The organisms were therefore defined in the model as controlling the flow of carbon to their skeletons rather than flowing that carbon through the organism compartments. Table I enumerates the preliminary working compartments identified for the CITRE model, with their acronyms and numbers.

Flows

In order that compartments may function within the model, they must be linked or coupled; flows (or fluxes) between them are measured in whatever is the currency of the model--i.e., the material with which exchanges are made. Flows, like compartments, are based on the general objectives of the modeling program. In the case of the CITRE model the following materials were considered significant to the model of a coral reef ecosystem: carbon, inorganic carbon, organic carbon, nitrogen, phosphorus, calcium, biomass, and energy. It was finally agreed to flow carbon through this model because of its mutual importance to the biochemical and geochemical cycles, even though other flows are also important. For example, the nutrients (PO_4, NO_3, etc.) which are important in feed-back loops controlled by photosynthesis, are flowed in the model, but for mathematical consistency, are converted to carbon equivalents.

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*Although there is no standard convention for naming compartments, flows, or other components, certain consistencies make bookkeeping easier and more accurate, such as the use of acronyms. Here X---- stands for compartment, thus XCBALG for CarBonate producing ALGae and XDON for Dissolved Organic Nitrogen. For convenience, all compartments were numbered consecutively as they appeared in the matrix (Fig. 9).

Forcing functions

Forcing functions are driving forces or variables which originate outside the system of reference but which influence the behavior of the system. These variables include light, temperature, inputs of materials, and other influences not under the control of the system.

The diagrams used in this model to illustrate compartments and flows are feedback dynamics or Forrester diagrams (Forrester, 1961). The units of compartments and flows in the CITRE model are grams of carbon per square meter (gC m^{-2}) and grams of carbon per square meter per day (gC m^{-2} day^{-1}) respectively. Figure 1 shows the symbols used in the diagrams and briefly describes meanings attached to these symbols. Although these diagrams may become very complex, they are useful for a graphic representation of the model and as a means to facilitate discussion. The general characteristics of the total CITRE ecosystem model as described by these diagrams is outlined below.

The forcing functions (external driving forces), compartments and flows between compartments, together delineate a preliminary total ecosystem model for a coral reef. Both the large number of compartments (104) and the number of flows between them form a very complex model.

Figure 2 graphically illustrates the couplings and ecological relationships of one compartment, the fleshy algae (XFLALG [5]). CO_2 input from XDISOL (80), a compartment of common interest to the Geology and Nutrients-Detritus groups, is controlled by four integrating functions, three of which (#1 through #3) are abiotic functions that regulate potential photosynthesis. Integrating function #4, coupled with the other three, gives realized photosynthesis. Dashed arrows from the integrating functions to the valves on the flows show that the integrating functions influence flow without contributing material to it, that is they are informational or control couplings rather than material flows or fluxes.

Six feedback loops or cyclical flows, of three basic types, affect this compartment. Two similar loops (diagrammed as one) indicate the cycling of carbon, or carbon equivalents of oxygen, respectively, between the dissolved organic carbon (XDOC [62]) or oxygen (XO2 [70]) compartments and XFLALG (5). These loops are controlled by the amount of the "upstream" or donor compartment present as well as by temperature, salinity, and exposure (integrating function #1). Another type of loop in the diagram shows the cycling of carbon to XTURF (4), XPHPL2 (12), and XPHPL3 (13). Flows to these three compartments from XFLALG (5) are reproduction, and flows back from them are recruitment from settling and growth. The third loop type is that diagramming CO_2 uptake from XDISOL (80) during photosynthesis, and its return during respiration.

Outputs to XDON (67) and XDOP (69) are excretion, as is in part the flow to XDOC (62).

Floating macroalgae, XDTPLT (8) break off from XFLALG (5) and continue living; detritus (XDETR3 [65] and XDETR4 [66]) is similarly derived.

XFLALG (5) also furnishes carbon to XBROWS (36), XGRAZV (48) and XBROWV (49), because these animals eat algae. The dotted arrows on this last set of flows show that these flows are controlled in part by the amount of algal material available, and in part by the biomass of the grazer.

Six more "single compartment" models are also shown in a similar diagram format (Figures 3-8). These diagrams all resemble Figure 2 in their complexity and mode of working. Space does not permit the inclusion of diagrams for all 104 compartments, although these were developed during the two-week workshop.*

Connectivity matrix

While feedback dynamics diagrams are a convenient method for showing individual compartments in detail, they cannot be combined for a model of this scale without becoming unmanageable mazes. An alternative graphical representation that has desirable properties is the connectivity matrix (Figure 9). This matrix is a square binary matrix showing the presence or absence of flows from each compartment to each other one. The size of the matrix is determined by the number of compartments (104 in the case of the CITRE model). Each compartment, from X1 through X104, is listed both across the vertical axis and down the horizontal axis. The direction of flow is from compartments on the horizontal to those on the vertical axis. Flows are indicated by a dot " " located at the intersection square of two components of the matrix. Thus, in Figure 9 for example, the single dot on the bottom line (XORGC 104) indicates a flow from XORGC (104) to XDOC (62) but not the reverse.

The connectivity matrix shows other information of interest. As its name implies, it illustrates the total "connectivity" or percentage of possible interaction. The CITRE matrix with 104 compartments has $(104)^2$ or 10,816 potential interactions. In this coral reef ecosystem model there are about 2,000 interactions or 20% connectivity. Since connectivity is highly dependent on compartment definition and at this level of resolution concerns only material flows, it is not possible to distinguish at this time between properties resulting from the modeling approach, and those inherent in the ecosystem. Complex ecosystems may be characterized by a much higher percentage of information "flows" or non-material interactions. However, these interactions are even more dependent than material flows on the level of model resolution.

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* Copies of the working drafts may be obtained from A. L. Dahl at Department of Botany, Smithsonian Institution, Washington, D. C. 20560. Some working groups are continuing to develop their parts of the model.

There are two disadvantages to the connectivity matrix: it does not show external forcing functions (temperature, currents, etc.) or information processing (which are shown by dashed arrows on the diagrams), and it does not indicate the magnitude of the flows.

A more complex form of matrix, a coefficient matrix, substitutes numerical values for the binary indicators of the connectivity matrix. Turnover rates then appear in the principal diagonal (a_{11}, a_{22}, a_{33},...) of the matrix, and flux or transfer rates appear in the off-diagonal elements. The CITRE matrix of turnovers and transfers is incomplete and is therefore omitted here.

While there is no immediate prospect of continuing to develop the CITRE model in its present form, it should now be possible to begin to piece together the major elements, and to quantify the essential relationships of the coral reef ecosystem. Only in this way will an overall picture of this most fascinating biological community ultimately be assembled.

Literature Cited

Forrester, J. W. 1961. Industrial dynamics. Cambridge, Mass.: MIT Press, 464p.

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
Benthic Plants (10)			
X1	Nitrogen-fixing algae	XNFIX	Probably important in reef nutrient cycling
X2	Coralline crusts	XCRUST	Important in forming and cementing reef framework through their calcium carbonate production
X3	Benthic microalgae	XBMALG	Primary unicellular forms in sediments and surface films
X4	Turf	XTURF	Composed of species such as Pterocladia, Polysiphonia, and Cladophora less than 2 cm. high
X5	Macro-algae, fleshy	XFLALG	Large fleshy algae over 2 cm. high, such as Turbinaria, Sargassum, and Dictyota that may produce significant macro-habitats
X6	Carbonate-producing macroalgae	XCBALG	Carbonate producing algae other than crusts, such as Halimeda, Rhipocephalus, Udotea, and Penicillus that make a significant contribution to carbonate sediments.

X7	Boring algae	XBORE	Includes filamentous and siphonaceous greens such as _Ostreobium_, that occur within the carbonate matrix of the reef and living animals.
X8	Detached plants	XDTPLT	Plants such as _Turbinaria_, _Sargassum_, _Thalassia_, and _Syringodium_ that often remain alive for some time as floating aglomerations, as well as _Acanthophora_ and _Laurencia_, that sometimes form drift populations on the bottom.
X9	Marine grasses - blades	XBLADE	The emergent portions of _Thalassia_, _Syringodium_, _Diplanthera_, and _Halophyea_
X10	Marine grasses - roots	XROOT	Roots and rhizomes of the seagrasses, as well as the portions of such algae as _Halimeda_, _Udotea_, _Rhipocephalus_, _Penicillus_, and _Avrainvillea_ that penetrate into the sediment
Plankton (23)			
X11	Heterotrophic phytoplankton	XPHPL1	Less than 10 u
X12	Autotrophic phytoplankton	XPHPL2	Less than 10 u

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Compartment Number	Compartment	Mnemonic Name	Characteristics
<u>Plankton</u> (23)			
X13	Autotrophic phytoplankton	XPHPL3	10-100 u
X14	Autotrophic phytoplankton	XPHPL4	Greater than 100 u
X15	Microholoplanktonic omnivores	XZOOH1	Less than 200 u
X16	Mesoholoplanktonic omnivores	XZOOH2	200-500 u
X17	Macroholoplanktonic omnivores	XZOOH3	Greater than 500 u
X18	Neuston omnivores	XZOON	All sizes
X19	Microepibenthic omnivores	XZOOE1	Less than 200 u
X20	Mesoephibenthic omnivores	XZOOE2	200-500 u
X21	Macroepibenthic omnivores	XZOOE3	Greater than 500 u
X22	Mesoholoplanktonic carnivores	XZOCH2	200-500 u
X23	Macroholoplanktonic carnivores	XZOCH3	Greater than 500 u
X24	Neuston carnivores	XZOCN	All sizes
X25	Mesoepibenthic carnivores	XZOCE2	200-500 u

X26	Macroepibenthic carnivores	XZOCE3	Greater than 500 u
X27	Microholoplanktonic detritus feeders	XZODH1	Less than 200 u
X28	Mesoholoplanktonic detritus feeders	XZODH2	200-500 u
X29	Macroholoplanktonic detritus feeders	XZODH3	Greater than 500 u
X30	Neuston detritus feeders	XZODN	All sizes
X31	Microepibenthic detritus feeders	XZODE1	Less than 200 u
X32	Mesoepibenthic detritus feeders	XZODE2	200-500 u
X33	Macroepibenthic detritus feeders	XZODE3	Greater than 500 u
Invertebrates (14)			
X34	Animal-plant symbionts	XHERM	Sedentary or sessile; derive a portion of their nutrition from symbiotic algae
X35	Invertebrate scrapers	XSCRAP	Motile animals that remove solid substratum along with food
X36	Invertebrate browsers	XBROWS	Motile animals that do not remove solid substratum along with food

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Compartment Number	Compartment	Mnemonic Name	Characteristics
X37	Passive suspension feeders	XAHERM	Sedentary or sessile; feed on materials suspended in the water column, passively collecting food brought by ambient water current
X38	Active suspension feeders	XSPONG	Sedentary or sessile; feed on materials suspended in the water column, actively create a water current to bring food through the food gathering apparatus
X39	Microbrowsers (meiofauna)	XMEIO1	Live on or in the sediment or reef framework and feed by passing sediment through their gut (all are less than 2 mm. in smallest diameter)
X40	Macro-deposit feeders	XDEPOS	Feeds by passing sediment through its gut (more than 2 mm in smallest diameter)
X41	Sedentary micropredators	XPRED1	Sessile or sedentary; capture individual prey organisms passing in the water.
X42	Predators on small prey	XPRED2	Motile animals that capture small invertebrates and/or vertebrates

X43	Predators on medium prey	XPRED3	Motile animals that capture medium-sized invertebrates and/or vertebrates
X44	Micropredators (meiofauna)	XMEIO2	Live within the sediment or in the reef interstices and capture small micro-browsers and/or other micro-predators.
X45	Parasites/pathogens	XIPARA	Relatively sedentary predator deriving its nourishment from one (or very few) prey individuals
X46	Parasite pickers	XPICKI	Motile animals that remove parasites from other animals
X47	Invertebrate eggs attached to reef	XBEGGI	Attached invertebrate eggs
Vertebrates (11)			
X48	Grazers	XGRAZV	Feed by scraping the substrate and in so doing remove a portion of the substrate
X49	Browsers	XBROWV	Feed by nipping the substrate but do not remove portions of the substrate
X50	Plankton feeders, bottom	XPLNKB	Feed on epibenthic plankton, regardless of their position in the water column

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Compartment Number	Compartment	Mnemonic Name	Characteristics
X51	Plankton feeders, midwater	XPLNKM	Feed on holoplankton neuston regardless of their position in the water column
X52	Predators, small	XPREDS	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size less than 50 mm standard length
X53	Predators, medium	XPREDM	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 51 mm to 250 mm standard length
X54	Predators, large	XPREDL	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 251 mm to 500 mm standard length
X55	Predators, top	XPREDT	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 501 mm and greater
X56	Parasite pickers	XPICKV	Feed on vertebrate ectoparasites
X57	Detritus feeders	XDETV	Feed on detritus

X58	Attached fish eggs	XBEGGV	Vertebrate eggs which are attached to the substratum or superstrate, brooded or guarded (i.e., non-pelagic)
Detritus/Nutrients (21)			
X59	NO_3	XNO3	Dissolved nitrate
X60	NO_2	XNO2	Dissolved nitrite
X61	NH_3	XNH3	Dissolved ammonia
X62	Dissolved organic carbon	XDOC	
X63	Suspended detritus	XDETR1	Smaller than 10 u
X64	Suspended detritus	XDETR2	10-100 u
X65	Suspended detritus	XDETR3	Greater than 100 u
X66	Trapped detritus	XDETR4	Detritus that falls to the bottom or moves by saltation along the bottom
X67	Dissolved organic nitrogen	XDON	
X68	Dissolved inorganic PO_4	XPO4	
X69	Dissolved organic P	XDOP	
X70	Dissolved O_2	XO2	
X71	Interstitial dissolved NO_3	XINO3	

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Compartment Number	Compartment	Mnemonic Name	Characteristics
X72	Interstitial dissolved NO_2	XINO2	
X73	Interstitial dissolved NH_4	XINH3	
X74	Interstitial dissolved organic C	XIDOC	
X75	Interstitial particulate organic C (dead)	XIDET	
X76	Interstitial dissolved organic N	XIDON	
X77	Interstitial dissolved organic P	XIDOP	
X78	Interstitial dissolved PO_4	XIPO4	
X79	Interstitial dissolved O_2	XIO2	
<u>Geology</u> (9)			
X80	Dissolved inorganic C	XDISOL	Grams carbon, dissolved in the seawater, in the form of CO_2, HCO_3- and CO_3. In motion.

X81	Suspended inorganic C.	XSUSP	Grams carbon, suspended in the seawater, in the form of fine $CaCO_3$. In motion.
X82	Bedload inorganic C	XBED	Grams carbon in the form of coarse $CaCO_3$. In motion, on or near the sea floor.
X83	Frame inorganic C	XFRAME	Grams carbon in the form of $CaCO_3$, representing the rigid framework of the reef
X84	Non-frame/non-sediment inorganic C	XORG	Grams carbon in the form of $CaCO_3$, tied up in living non-frame organisms
X85	Inorganic C in rubble	XRUBBL	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment. Greater than 4 mm.
X86	Inorganic C in sand	XSAND	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment, 62 u-4 mm
X87	Inorganic C in mud	XMUD	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment less than 62 u.
X88	Interstitial dissolved	XH2O	Grams carbon dissolved in the interstitial waters of the sediment in the form of CO_2, HCO_3 and CO_3.

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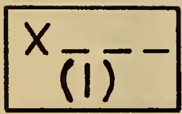
Compartment Number	Compartment	Mnemonic Name	Characteristics
Terrestrial Phenomena (16)			
X89	Photosynthetic plants	XPPHOT	Agents of primary productivity of carbohydrates
X90	Nitrogen-fixing plants	XNFIXP	Remove N_2 from the atmosphere and add it to the nutrient pool
X91	Nitrogen-transforming plants	XTRAN	Oxidize or reduce nitrogen compounds
X92	Decomposing plants	XPDECM	Convert all other organisms or organic materials into available nutrients, CO_2, and water
X93	Seabirds	XSBIRD	Eat fish from the reef and from the open ocean, and thus transfer nutrients to the cay system from both these sources
X94	Decomposing animals	XADECM	Active in reducing the complex compounds of which plant and animal material is made into soluble, available compounds useful as nutrients for autotrophic plants
X95	Other land animals	XALAND	Herbivores, carnivores, and predators

X96	Nitrogen	XNIT	Dissolved N compounds existing in soil-water and in ground-water
X97	Phosphorus	XPHOS	Exists in calcium carbonate deposits in cay sediments and in soluble forms in soil- and ground water
X98	Calcium	XCAL	Dissolved from sediments and brought in by spray and in bird excrement
X99	Potassium	XPOTAS	In salt spray and in plant and animal detritus and bird excreta
X100	Other mineral nutrients	XMINER	Elements essential in small or trace amounts
X101	Soil water	XSURWT	Interstitial water and films on soil particles
X102	Ground water	XGRDWT	All free liquid freshwater in the system, in the form of a Ghyben-Herzberg lens within the mass of cay sediments
X103	Sediments	XSED	Cays are entirely constructed of sediments that originated on the reef
X104	Organic C	XORGC	Dissolved organic matter leached from or excreted by plant and animal tissues or wastes

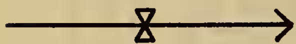
Figure 1

Symbols for feedback dynamics diagrams

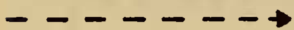


Designates a compartment, or a functional group (gC m^{-2}).

Material flow. This would be fluxed grams carbon or nutrients (gC m^{-2} day^{-1}).

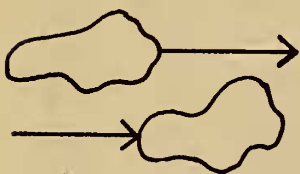


Flows are controlled by "valves".

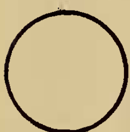


A dashed line is information.

This symbol is a decision function, which serves to integrate information about influences on a flow.



In addition to flows between compartments, material may come from a source, external to the system of definition, or be sequestered in an external sink.



An open circle with a name in it is a variable which comes from outside the system of reference (e.g., sunlight).

This symbol is used in the illustration of small compartment groupings or submodels to show flow from a compartment within the system of definition, but not of interest in the present diagram.

This symbol shows a flow from a compartment to another compartment within the system of definition but not of interest in the present diagram.

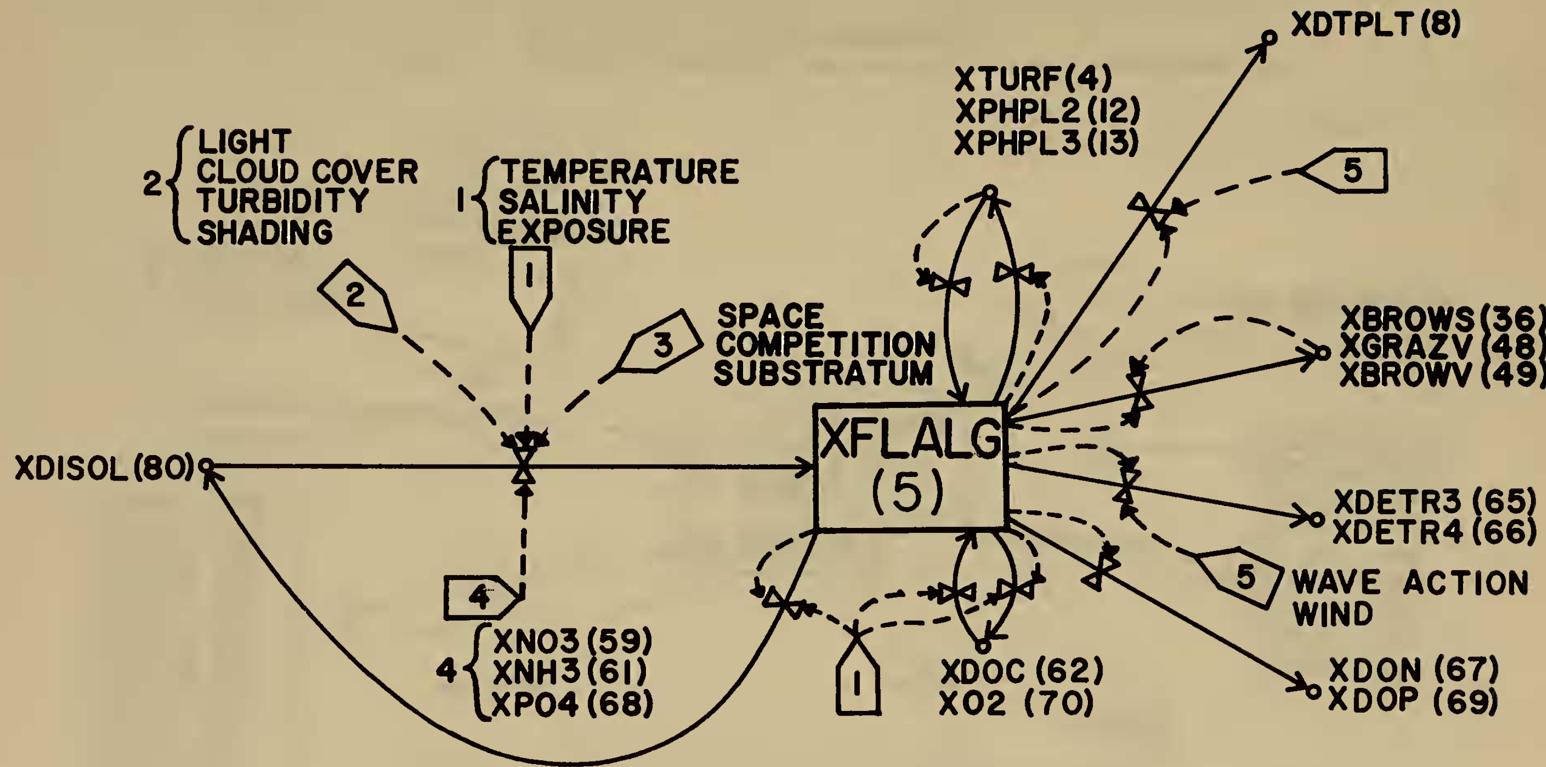


Figure 2. Diagram representing the fleshy macro-algal compartment and its relation to other compartments.

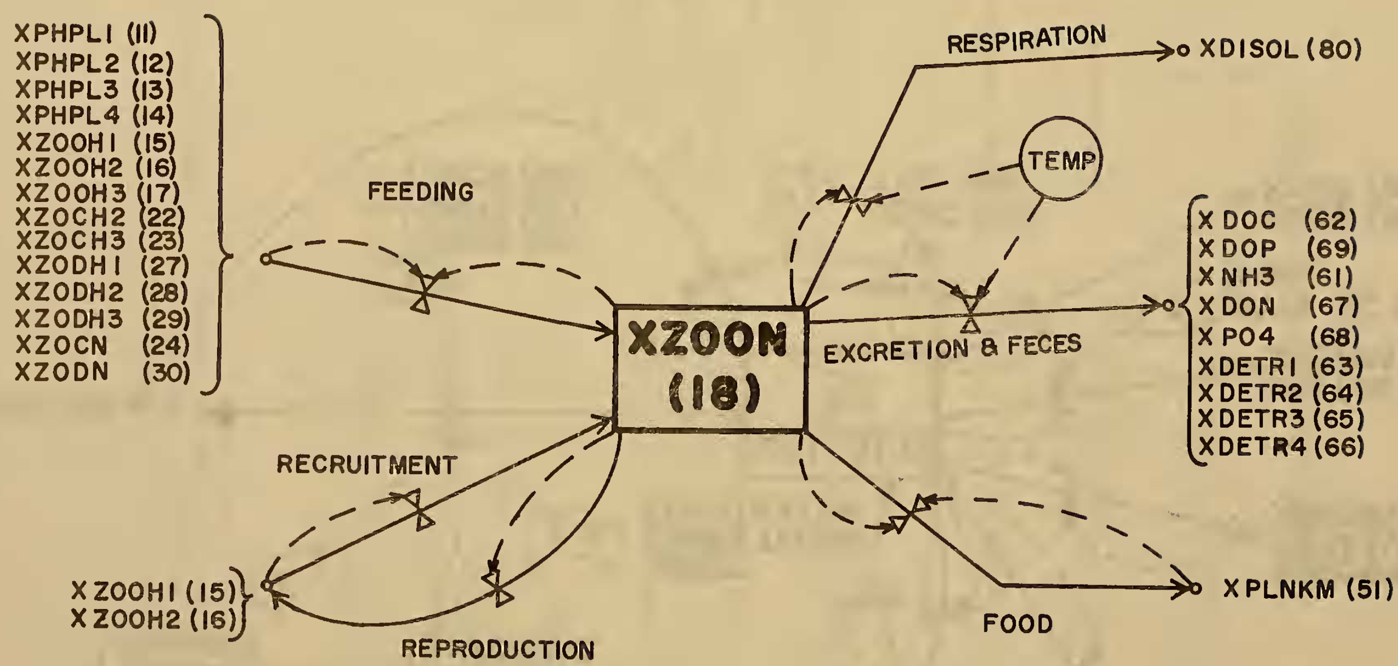


Figure 3. Diagram representing the neuston omnivore compartment and its relation to other compartments.

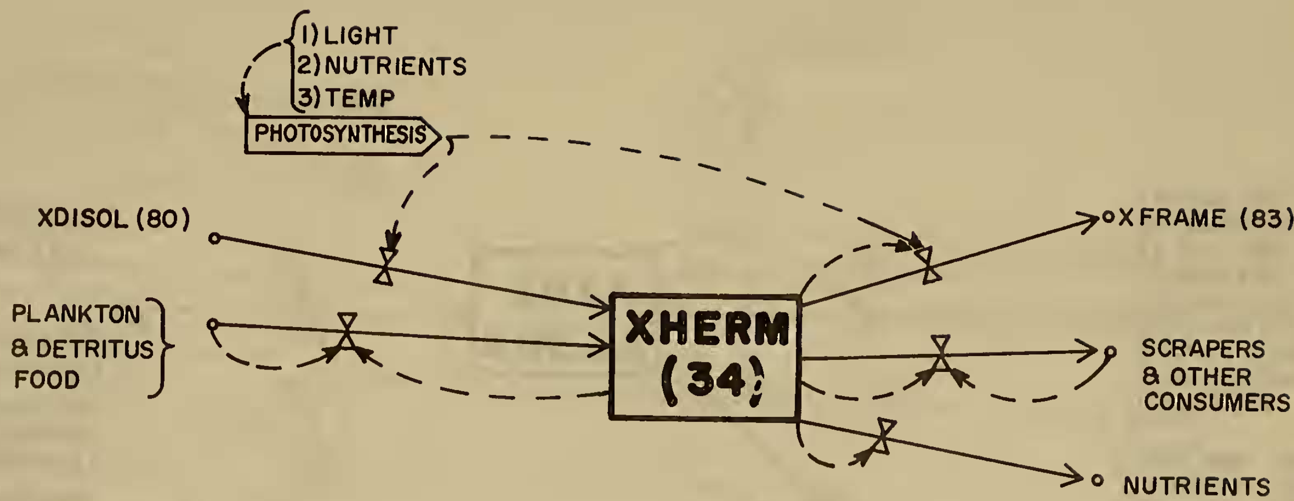


Figure 4. Diagram representing the animal-plant symbiont (hermatypic coral) compartment and its relation to other compartments.

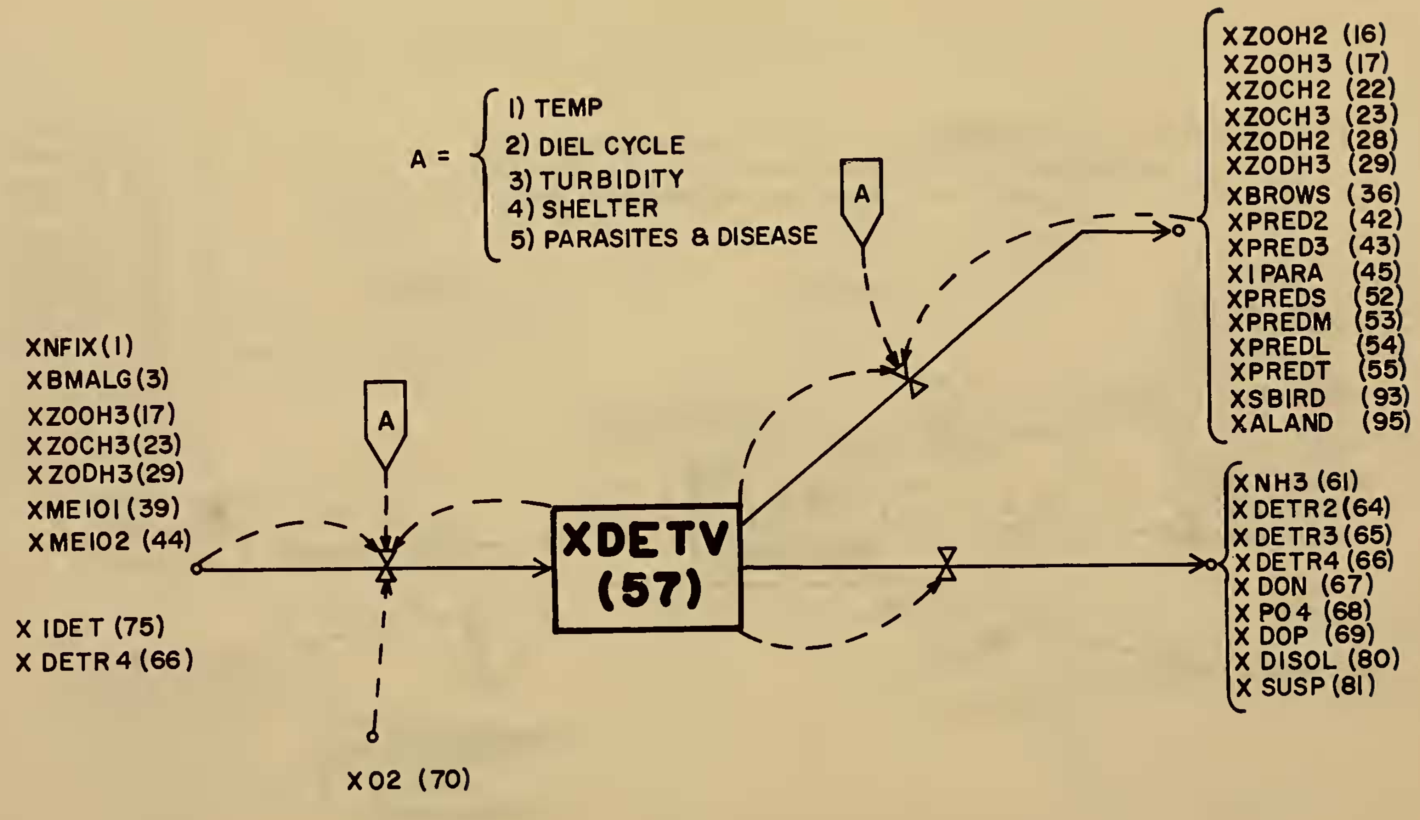


Figure 5. Diagram representing the detritus feeder compartment and its relation to other compartments.

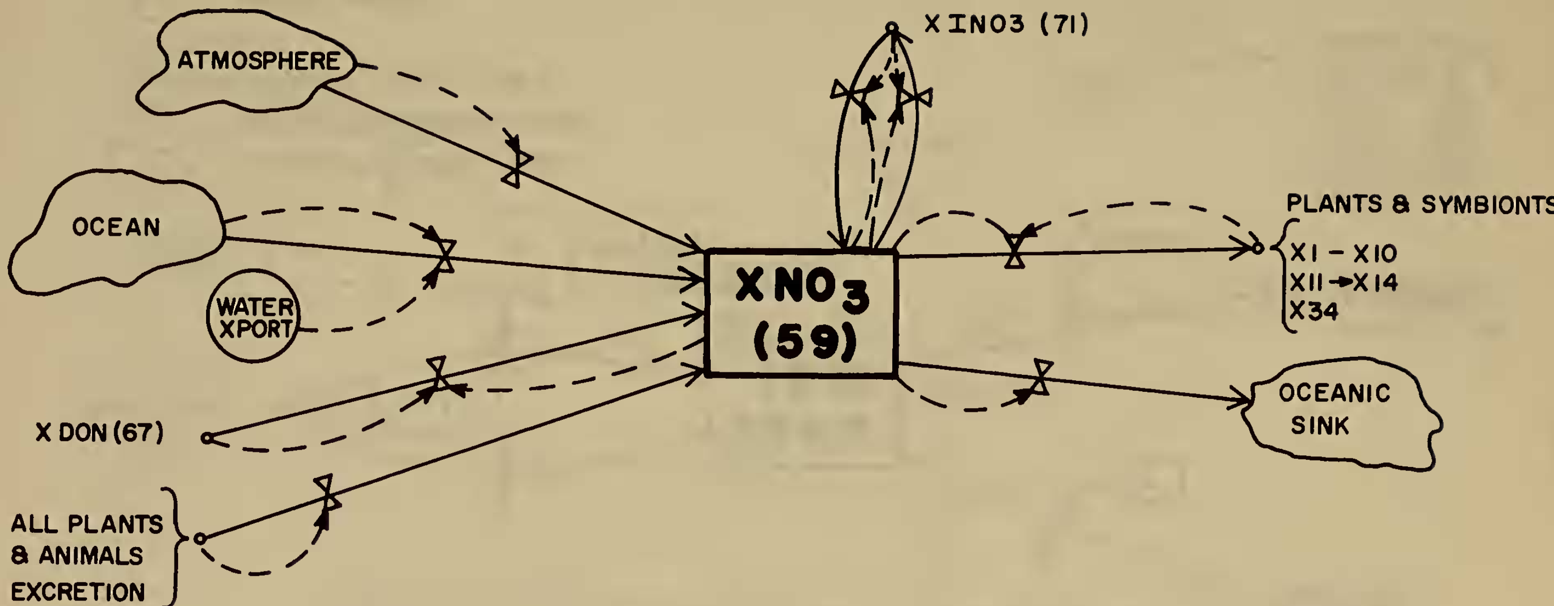
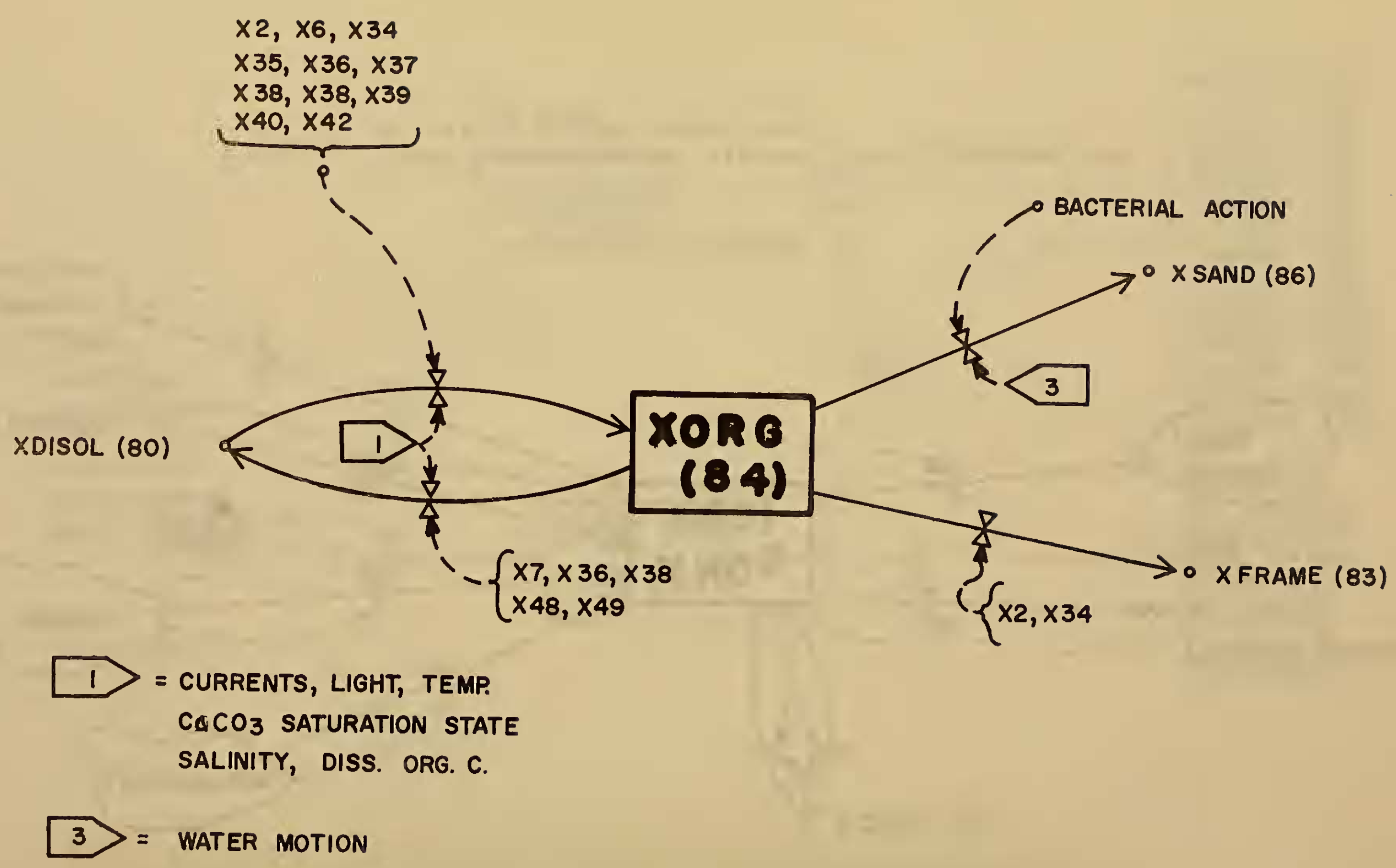


Figure 6. Diagram representing the dissolved nitrate compartment and its relation to other compartments.



<u>Figure 7.</u> Diagram representing the non-frame/non-sediment $CaCO_3$ compartment and its relation to other compartments.

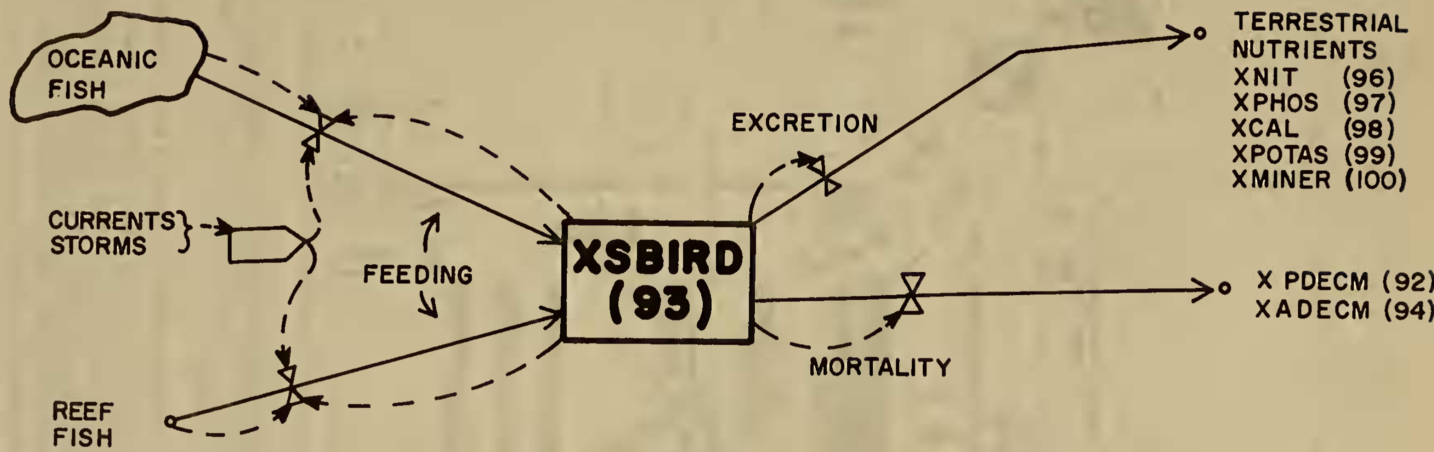


Figure 8. Diagram representing the seabird compartment and its relation to other compartments.

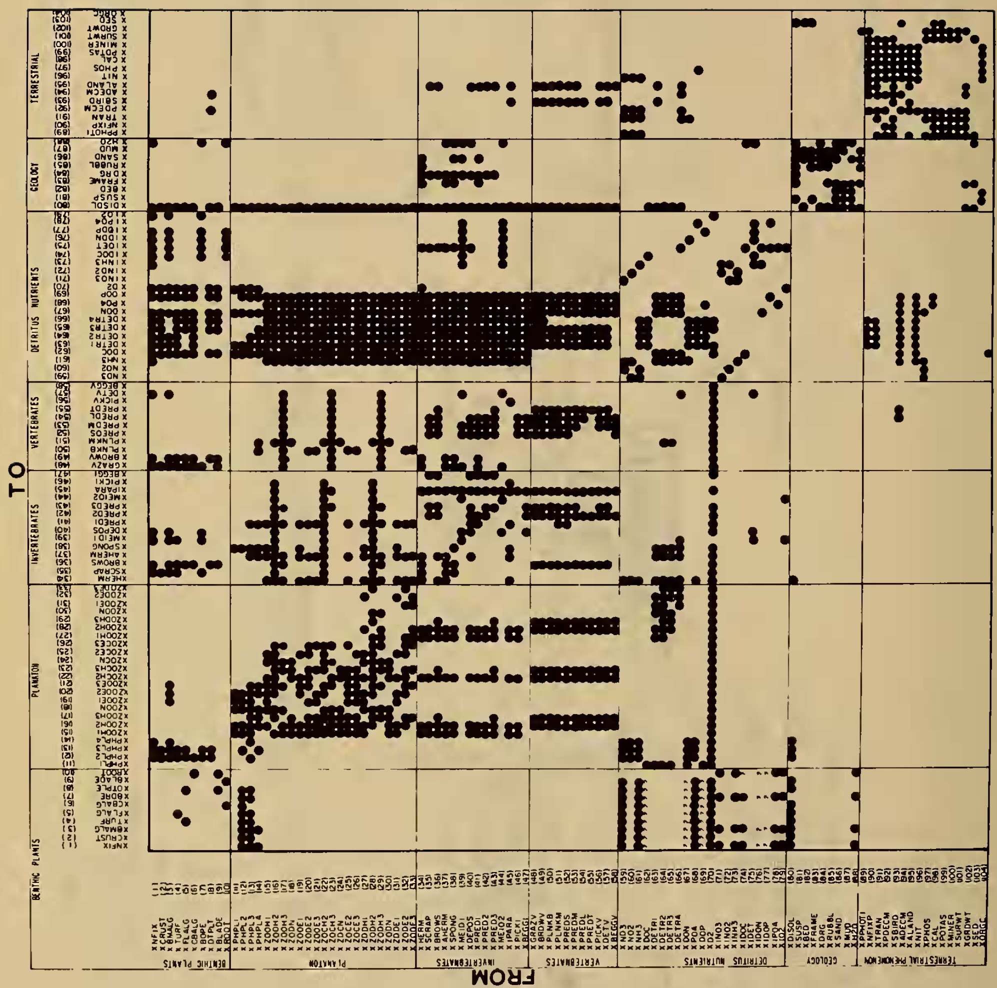


Figure 9. CITRE preliminary ecosystem matrix; reef-flat submodel. The dots indicate carbon or carbon-equivalent flows from compartments on the left to compartments along the top. Blanks indicate no connectivity, and the question marks indicate possible carbon flow between various organic compounds and benthic plants.

A COMPARATIVE SURVEY OF CORAL REEF RESEARCH SITES*

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The complexity of coral reef environments has long attracted scientific interest, but as yet few if any research programs have compared reefs from different areas or oceans with a view to understanding the overall functioning of a reef ecosystem. Plans for such programs recently were initiated at the Smithsonian Institution, and it was found that in the undertaking of an interdisciplinary investigation of reef ecosystems, the first critical step is to choose research sites that can meet stringent scientific criteria.

The Smithsonian's comparative information on potential reef research sites in both the Caribbean and Pacific is being presented here in the hope that other investigators will find it useful in planning future reef studies. The data were originally compiled as a report on the research site selection process for the Smithsonian programs, and this has largely determined the present format. The observations are primarily qualitative in nature, presenting a broad view of comparative reef structure and composition. Their value lies in their common perspective, having been compiled by a closely integrated site selection team whose members, within a short time, visited many coral reef areas throughout the Caribbean and much of the Pacific, applying common criteria to achieve a common goal.

The site search was conducted for two programs of the Smithsonian Institution. The first, Investigations of Marine Shallow Water Ecosystems (IMSWE), was organized within the National Museum of Natural History with the support of the Smithsonian Environmental Sciences program to conduct an integrated biological and geological analysis of coral reef communities. The second was to be a much larger, multi-institutional program, the Comparative Investigations of Tropical Reef Ecosystems (CITRE), developed under the auspices of the Smithsonian Office of Environmental Sciences with a planning grant from the International Decade of Ocean Exploration Office at the National Science Foundation. The plans for the CITRE program included the development of a complete systems analysis model of the reef ecosystem based on energy and material flows through various reef components. For both programs, the scientific advantages and greater research potential of a scientifically "ideal" reef site were given first priority, with purely logistical considerations

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considered secondarily, and thus a fresh look was taken at many potential reef research areas with the context of the programs in mind. An "ideal" reef was considered to be one that is subject to little external stress, and that is characterized by as many of the scientific criteria as possible.

Since the criteria by which sites were judged have a crucial bearing on the conclusions of the site analysis, they are outlined below in some detail:

1. Ample development of all characteristic reef zones, from the "reef flat" to deep water communities in depths of 50 to 100m.

2. A steep fore-slope, to facilitate field observations by telescoping the zonation.

3. Vigorous reef growth where interactions with the surrounding water mass can be measured and with a good geological record of past development.

4. Unidirectional current flow for periods long enough to permit cross-reef metabolic studies of the type successfully used at Eniwetok (Johannes _et al_. 1972).

5. No overriding unique characteristics with respect to the reefs in the same area.

6. Freedom from major terrestrial, human, or natural catastrophic influences in the present or recent past.

Some practical criteria could not be ignored:

1. Sufficient accessibility to meet the needs of a large program.

2. A harbor and some accommodations and facilities, or the possibility of developing these at reasonable cost.

3. Availability of research vessel support.

4. Probability of a stable government with a favorable attitude towards the program.

5. Suitability for research needs such as multiple sampling, monitoring with shore-based instrumentation, drilling for geological samples, etc.

Since the published literature has only scattered information on many of these features, a questionnaire (Fig. 1) was developed and sent to numerous scientists with field experience in the Caribbean and the tropical Pacific. The response was generally good, particularly for the Caribbean, and provided many suggestions for potential coral reef research sites. Following preliminary evaluation of the questionnaires, survey teams were sent to the most promising reef areas to investigate